

Prokopocrinidae, New Family of ?Camerate Crinoids, Silurian (Wenlockian-Ludlovian), Tennessee and Oklahoma

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ABSTRACT

The new Silurian platycrinitacean crinoid genus *Prokopocrinus* represents an extreme in calyx simplification among camerates. Perfectly pentamerously symmetrical aside from the tripartite base, these diminutive (width 1.4–1.8 mm) monocyclic crinoids lack interradians and anal plates or other indicators of the position of the anal opening and can be oriented only by reference to the azygous basal (located in EA interray?). The family Prokopocrinidae (nov.) probably are descended from the Hirneocrinidae, culminating a trend in the superfamily Platycrinitacea toward expulsion of the interradians (including the primanal) from the cup.

The Prokopocrinidae differ from the Hirneocrinidae and Hapalocrinidae in their small size, and lack of both a differentiated CD interray and of interradians (IRR) participating in the calyx; hence these crinoids cannot be assigned to existing families. Parallel evolutionary trends in the inadunate orders Disparida (monocyclic; microcrinoids and an undescribed hapalocrinitid) and Cladida (dicyclic; *Elicrinus* Prokop, 1973) produced similar-appearing genera; assignment of the family to the Camerata is not indubitable.

Three new species are placed in *Prokopocrinus*: *P. tuberculatus*, the type species, is a depressed bowl-shaped form with tumid plates, impressed plate sutures, and irregularly developed tuberculate surface. *P. laevis* is characterized by a deeply bowl-shaped cup and smooth plates without impressed sutures. These 2 species are from the Henryhouse Formation (Ludlovian), Oklahoma. *P. barricki* (Wenlockian; Waldron Shale, Tennessee) has a basal flange, pentalobate calyx, and unevenly pitted ornamentation (prosocon). All 3 were members of a sparse, relatively deep-water crinoid assemblage typified by an abundance of *Pisocrinus*, *Lecanocrinus* and other flexibles, calceocrinids, and microcrinoids. The small size of *Prokopocrinus* and associated taxa, plus preservational factors, suggest a soft-bottom habitat with a slow or moderate sedimentation rate and weak currents. The assemblage is possibly analogous to the *Dicoelosia-Skenidioides* Community of Benthic Assemblage 4 of Boucot (1975).

The echinoderm fauna of the classic Waldron Shale (Wenlockian) localities in Indiana has been fairly well known for almost a century (Hall, 1879); not so the echinoderms of equivalent strata in Tennessee. An analogous situation obtains for the Henryhouse Formation (Ludlovian) of Oklahoma; the crinoids of the typical facies were monographed by Strimple (1963), but those from what we interpret as a deeper water facies have been neglected. Crinoids recovered recently from some Waldron and Henryhouse shale samples are significantly different from those of well-known locali-

ties. Common to both formations are abundant pisocrinids and calceocrinids, microcrinoids, and *Lecanocrinus*. Rare are the large camerates normally quite common in both. The Henryhouse sample has abundant *Gissocrinus*; this genus has not been found in the Waldron, but small *Stephanocrinus* is exceedingly abundant.

Brachiopods and ostracods are the only other common invertebrate groups. Fewer than the usual complement of brachiopod genera are present; *Dicoelosia* is quite abundant. Almost all the crinoids and brachiopods are small;

many of the crinoids fall into the microcrinoid and minicrinoid (term defined herein) size ranges, being less than 5 mm in width. The crinoids described below exemplify this observation; though fully adult, none exceed 2 mm in diameter. This has unfortunately precluded photographic illustration of the new taxa, and camera lucida sketches are used instead. Also hampering taxonomic treatment is the rarity of complete calices (isolated radials are common) and the simple structure of many of the new crinoids. Large-scale bulk processing has not been attempted; though shaley, the samples can be only partially disaggregated by standard procedures. No crowns have yet been recovered, and isolated skeletal elements are many times more abundant than articulated calices.

The extremely simple nature of the calyx plate configuration of the crinoids herein named *Prokopiecrinus* makes it impossible to assign them unequivocally even to subclass level. Nevertheless, recent work on the early history of the divergent camerate superfamilies Patelloocrinacea and Platycrinacea allows placement of the new genus and family in the latter with some confidence. Well known phylogenetic trends within the two superfamilies (Brower, 1973; Frest and Strimple, 1977) reach their apogee in the Prokopiecrinidae; the existence of such forms could easily have been predicted from previously known information. Convergent evolution produced similar forms in the Inadunata at about the same time; these crinoids are, fortunately, not perfect homeomorphs of the Prokopiecrinidae and can be separated from the camerates on various grounds.

All specimens have been placed in the Repository, Department of Geology, University of Iowa.

Systematic Descriptions

Class CRINOIDEA Miller, 1821

Subclass CAMERATA Wachsmuth
and Springer, 1885

Order DIPLOBATHRIDA Moore and
Laudon, 1943

Superfamily PLATYCRINITACEA Austin and
Austin, 1842

Diagnosis.—Calyx tending to be confined to lowermost 2 plate circlets (patina); basals (BB) 3, unequal (small one normally in AE interray) or fused; brachials and interbrachials generally little or not at all represented in calyx. Proximal brachials tending to stand out clearly from radials (RR) although joined firmly to calyx, tegmen, or both by interradially situated plates in primitive members; interradians absent in advanced members; posterior side slightly or not differentiated in calyx (adapted from Ubaghs, 1978).

Range.—U. Ordovician—Permian, worldwide.

Included families.—Platycrinitidae Austin and Austin, 1842; Hapalocrinidae Jaekel, 1895; Hirneocrinidae Frest and Strimple, 1977; Prokopiecrinidae (nov.).

Remarks.—Our concept of the Platycrinacea is essentially identical to that promulgated by Ubaghs (1978) except for a few points. We place the Marsupiocrinidae in the Patelloocrinacea, rather than the Platycrinacea; the rationale for our preference is given in Frest and Strimple (1978). Addition of the Hirneocrinidae and Prokopiecrinidae to the superfamily since Ubaghs' work was written necessitates minor emendation of his superfamilial diagnosis. The additional two families represent the culmination of certain phylogenetic trends first recognized by Brower (1973) but implicit in Ubaghs' diagnosis within the closely related Patelloocrinacea and Platycrinacea. Most important is a tendency to reduce the calyx to a patina of BB and RR; concomitantly the IRR and anals disappear or are expelled from the calyx onto the tegmen, the arms may become completely free at the RR, and near perfect pentameral symmetry is achieved.

None of the half dozen *Prokopiecrinus* specimens thus far recovered preserve the tegmen; this is analogous to the situation in the Hirneocrinidae (Frest and Strimple, 1977). Its lack of prominence can be inferred readily from the observation that the edges of the RR extend onto the oral surface, covering

much of it (figs. 3, 6, 9). This arrangement is also duplicated in the Hirnecrinidae and suggests that only a small number of plates constituted the tegmen and that the structure was loosely sutured. If so, this contrasts strongly with the multi-plated, prominent, and rugged tegmen characteristic of the Platycrinidae and militates against that family as ancestral to the Prokopocrinidae.

Family PROKOPICRINIDAE, new family

Diagnosis.—Calyx diminutive, pentagonally symmetrical, bowl-shaped, confined to patina of 5 RR and three unequal BB, small B in AE interray; posterior side not differentiated, tegmen not prominent. Column round, homeomorphic. Arms and tegmental plating unknown.

Included genus.—*Prokopicrinus*, new genus.

Range and distribution.—M.—U. Silurian (Wenlockian-Ludlovian), Tennessee and Oklahoma.

Remarks.—The Prokopocrinidae is closely related to at least 2 platycrinitacean families. It differs from the Hirnecrinidae in that the latter still has IRR notching the RR and a differentiated CD (posterior) interray. Crinoids of the Platycrinidae are generally large, have a prominent dome-shaped tegmen, and possess elliptical and twisted synarthrially articulated columns (Lane, 1978; Broadhead and Strimple, 1977). Such features as stratigraphic range, reduced tegmen and IRR, plus the infolded tops of the RR support direct descent from the Hirnecrinidae, rather than either independent origin from the Hapalocrinidae or derivation from supposed early platycrinitids.

Though quite small, these crinoids are adults; no larger calices or isolated plates have been found despite protracted search. We do not consider *Prokopicrinus* a microcrinoid. Though the term "microcrinoid" (*sensu lato*) can embrace a fairly wide size range (Arendt, 1970) we prefer to restrict it to those crinoids having a considerable part of their potentially preservable ontogenetic

development taking place at sizes below 1 mm: such crinoids, we believe, constitute a homogenous group unrelated to the presently considered forms. For those macrocrinoids that are unusually small we propose the term minicrinoid. Arbitrarily a maximum adult "size" (A ray-CD interray width at tops of RR) of 5 mm is a convenient breaking point while a minimum in excess of 1 mm (for the youngest calcified stages) can be used to delimit the lower end of the minicrinoid size range. This small size very probably has functional consequences. Many, if not all, minicrinoids may have been competing primarily with microcrinoids and may have been capable only of tentacular or limited mucus-net feeding, analogous to the pentacrinoid larval stage of modern Articulata.

The simple structure of the calyx and, especially, the lack of a differentiated anal side makes orientation difficult. Lacking morphologic criteria we fall back on phylogeny. The system adapted here (figs. 1, 12) is based on the assumption that the genus is a platycrinitacean and hence has the small basal in the AE interray—a defensible but hard to prove contention.

Genus *Prokopicrinus*, new genus

Figures 1, 12

Diagnosis, range, and distribution are the same as those given for the family.

Type species.—*Prokopicrinus tuberculatus*, n. sp., Henryhouse Formation (Ludlovian).

Derivation of name.—We take considerable pleasure in naming this genus after Rudolph J. Prokop, Narodni Muzeum, Czechoslovakia.

Prokopicrinus tuberculatus, new species

Figures 9–11

Diagnosis.—Calyx depressed, much wider than high; BB barely visible in side view; plates tumid, irregularly tuberculate, sutures deeply impressed; prosopon consists of numerous small tubercles, irregular in size and arrangement; no basal flange.

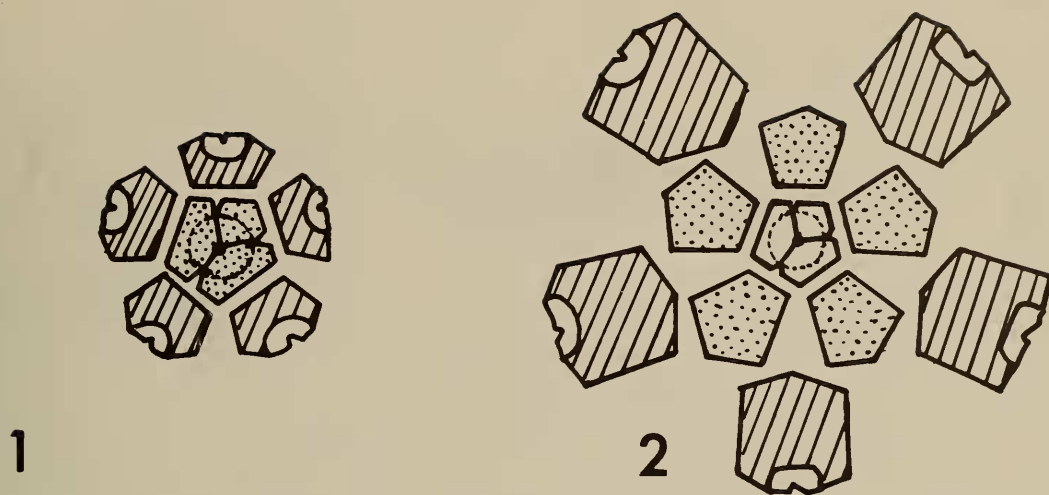


Fig. 1-2. Plate diagrams: 1, *Prokopocrinus*; 2, *Elicrinus*. Infrabasals white, basals dotted, radials obliquely lined. Presumed A ray uppermost.

Material.—A single specimen, the holotype (SUI 44341), recovered from weathered material derived from the upper part of the Henryhouse Formation, NW 1/4 NW 1/4 SW 1/4 sec. 33, T 3 N, R 6 E, Ahloso quadrangle, Pontotoc County, Oklahoma.

Description.—Calyx outline rounded to pentagonal due to slight protrusion of R arm facets and tumid plate centers; calyx small (see in Table 1), depressed bowl-shaped. BB 3; 2 equal, 5 sided in plan view (fig. 11), centered in B and D rays; smaller B (in AE interray) 4 sided in bottom view; B circlet small, about 1/3 maximum calyx diameter, pentagonal, barely visible in side view (fig. 10). Stem facet protruded slightly, circular, 1/2 width of B circlet; lumen small, circular. RR 5, equal, making up most of calyx height, upper edges extending onto oral surface and covering approximately 3/5 of its area. Arm facets semicircular, peneplenary, declivate, surrounded by indistinct rim; axial canal not separate. Arms and tegmen unknown. Plates thick, tumid, with moderately impressed sutures; outer plate surfaces covered irregularly with variously sized, low rounded tubercles. The tumidity of the BB gives the impression of an insignificant basal flange.

Derivation of name.—Suggested by plate ornament.

Remarks.—*P. tuberculatus* somewhat resembles *P. barricki* in calyx shape but the details of plate thickness, ornament, and other characters are distinctive. From *P. laevis* the species can be differentiated by the less prominent BB as well as the surficial differences indicated by the trivial names. The calyx shape and large arm facets are superficially similar to those of *Hirneacrinus*. The species is much larger than the remaining 2 (Table 1).

Prokopocrinus laevis, new species
Figures 6-8

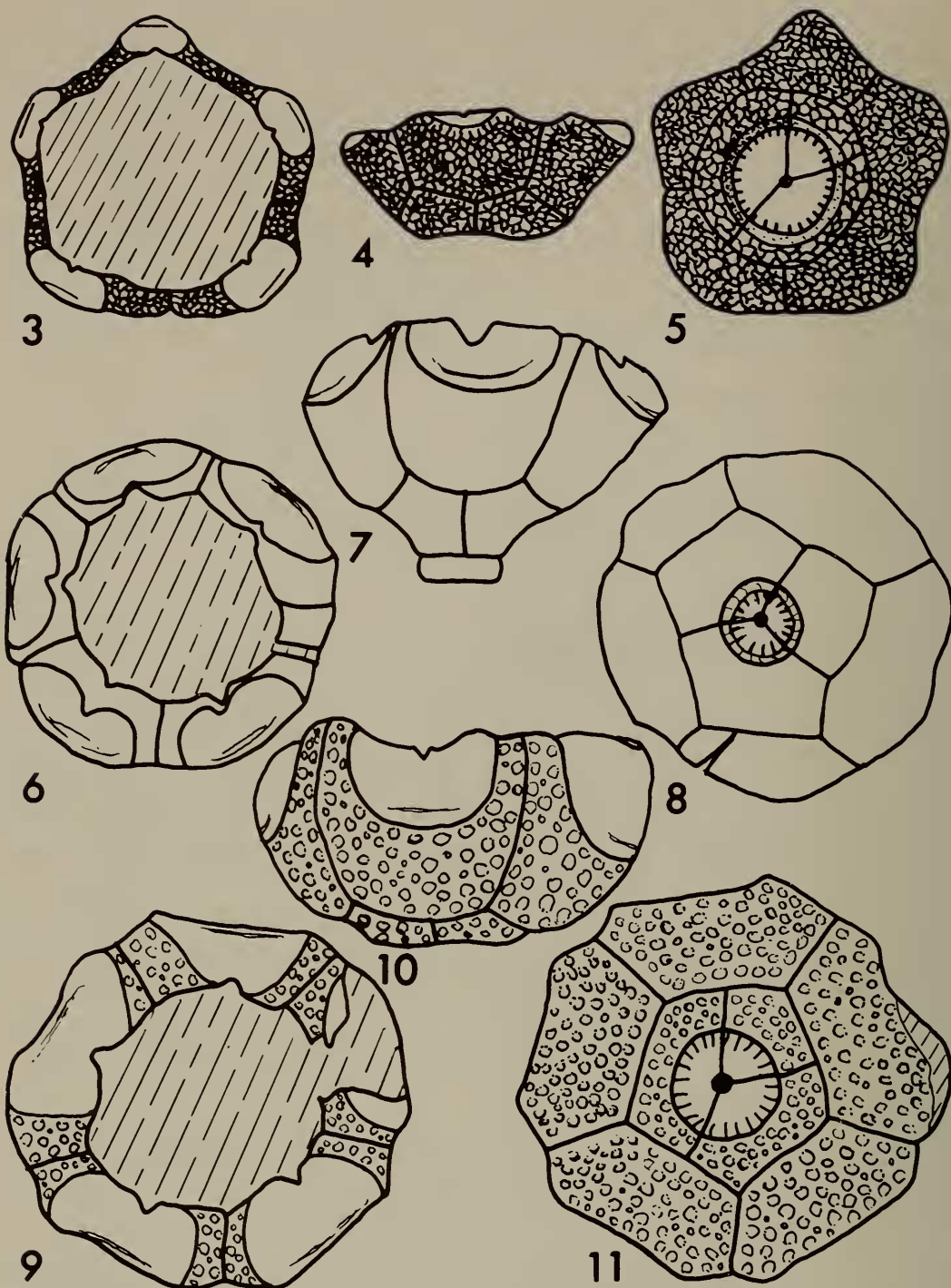
Diagnosis.—*Prokopocrinus* with only slightly wider than high, bowl-shaped calyx having prominent (in lateral view: fig. 7) BB and smooth plates without impressed sutures. No B concavity or flange.

Material.—An isolated calyx lacking the tegmen; one radial fractured. Provenance same as preceding species; holotype SUI 44340.

Description.—Calyx outline subcircular except for barely perceptible protrusion of R arm facets (figs. 6, 8); diminutive (see Table 1), only slightly

Table 1.—Measurements of *Prokopocrinus* species (holotypes).

Name	A-CD Width	Height	Diameter of column facet	H/W ratio	Calyx width/column facet width
<i>P. tuberculatus</i>	1.83 mm	1.07 mm	0.50 mm	0.55	3.66
<i>P. laevis</i>	1.56 mm	1.10 mm	0.40 mm	0.71	1.42
<i>P. barricki</i>	1.43 mm	0.57 mm	0.47 mm	0.40	2.51



Figs. 3–11. Camera lucida drawings of holotypes of *Prokopiecrinus* species: 3–5, *P. barricki*, n.sp. (SUI 44338); 6–8, *P. laevis*, n.sp. (SUI 44340); 9–11, *P. tuberculatus*, n.sp. (SUI 44341). Each set consists of a top, side, and bottom view; all drawings $\times 25$.

wider than high. B circlet roughly pentagonal; B shapes and orientation as in *P. tuberculatus*; circlet wide ($\frac{1}{2}$ calyx width as viewed from below), distally protruded from calyx into stem facet, making up about $\frac{1}{3}$ of total calyx height (fig. 7). Stem facet circular, narrow (less than $\frac{1}{4}$ greatest calyx diameter); holotype retains a single narrow cylindrical columnal with small circular lumen and crenularium not prominent; 5 equal RR infolded onto the oral surface in a manner and degree comparable to *P. tuberculatus* (fig. 6); arm facets semielliptical, declivate, much wider than

high, approaching full width of RR, notched proximally by combined axial canal and ambulacral tract; subdued rim around distal perimeter. Plates smooth, thick but not tumid, sutures not impressed. No suggestion of basal flange. Arms and tegmen unknown; latter would roof less than half of the flattened oral surface.

Derivation of name.—The specific epithet refers to the unornamented plates.

Remarks.—*P. laevis* is most comparable to *P. tuberculatus*; specific differences have been noted under the latter's description.

Prokopocrinus barricki, new species
Figures 3–5

Diagnosis.—A species of *Prokopocrinus* characterized by its pentalobate calyx (figs. 4, 6), basal flange and accompanying narrow basal concavity, and pitted plate surfaces.

Material.—Three calices (holotype SUI 44338; unfigured paratypes SUI 44339), from a sample of Waldron Shale collected by James Barrick, University of Iowa. The sample was obtained from an 8 cm thick shale bed immediately above the Waldron-Laurel contact in the abandoned Franklin Limestone Company quarry north of Clifton, Wayne County, Tennessee (Clifton 7½' quadrangle: Tennessee coordinates 378,000N, 1,412,250E).

Description.—Calyx small (less than 1.5 mm wide: see Table 1), pentalobate in plan view, wider than high; holotype more flat based and depressed than paratypes. Outline of B circlet rounded, only faintly pentagonal (fig. 5). BB prominent in side view (fig. 4), distally produced into basal flange surrounding comparatively wide ($\frac{1}{3}$ calyx diameter) column facet. The circular stem facet is impressed into BB; B concavity has narrow periphery separating stem facet from basal flange. RR 5, large, much wider than high, overlapping oral surface less than in other *Prokopocrinus* species (fig. 3), produced into broad lobes strongest near center of upper edges. Arm facets narrow, almost quadrangular in shape, not exceeding $\frac{1}{2}$ greatest R width; orientation nearly horizontal. Facets on lobate portion of RR, notched by axial canal-ambulacral tract. All calyx plates with coalescing, irregularly polygonal, shallow pits; plate sutures not impressed. Proximal columnals (removed in cleaning) short cylinders with tiny circular lumen; crenularium distinct, simple, narrow. Arms and tegmen not preserved.

Derivation of name.—The species name honors the collector, James Barrick.

Remarks.—Calyx shape, atypically wide tegmental region, and narrow arm facets suggest that *P. barricki* is more distantly related to *P. laevis* and *P. tuberculatus* than the 2 latter species are to each other. Too little is known about the phylogenetic significance of specific taxobases in *Prokopocrinus* to permit evaluation of interrelationships

at the species level. The peculiar surface features, reminiscent of the outside surface of hammered aluminum kitchen ware, are rare among crinoids; the unrelated disparid inadunate *Apodasmocrinus punctatus* (Brower and Veinus, 1974) is the closest parallel.

Paleoecology

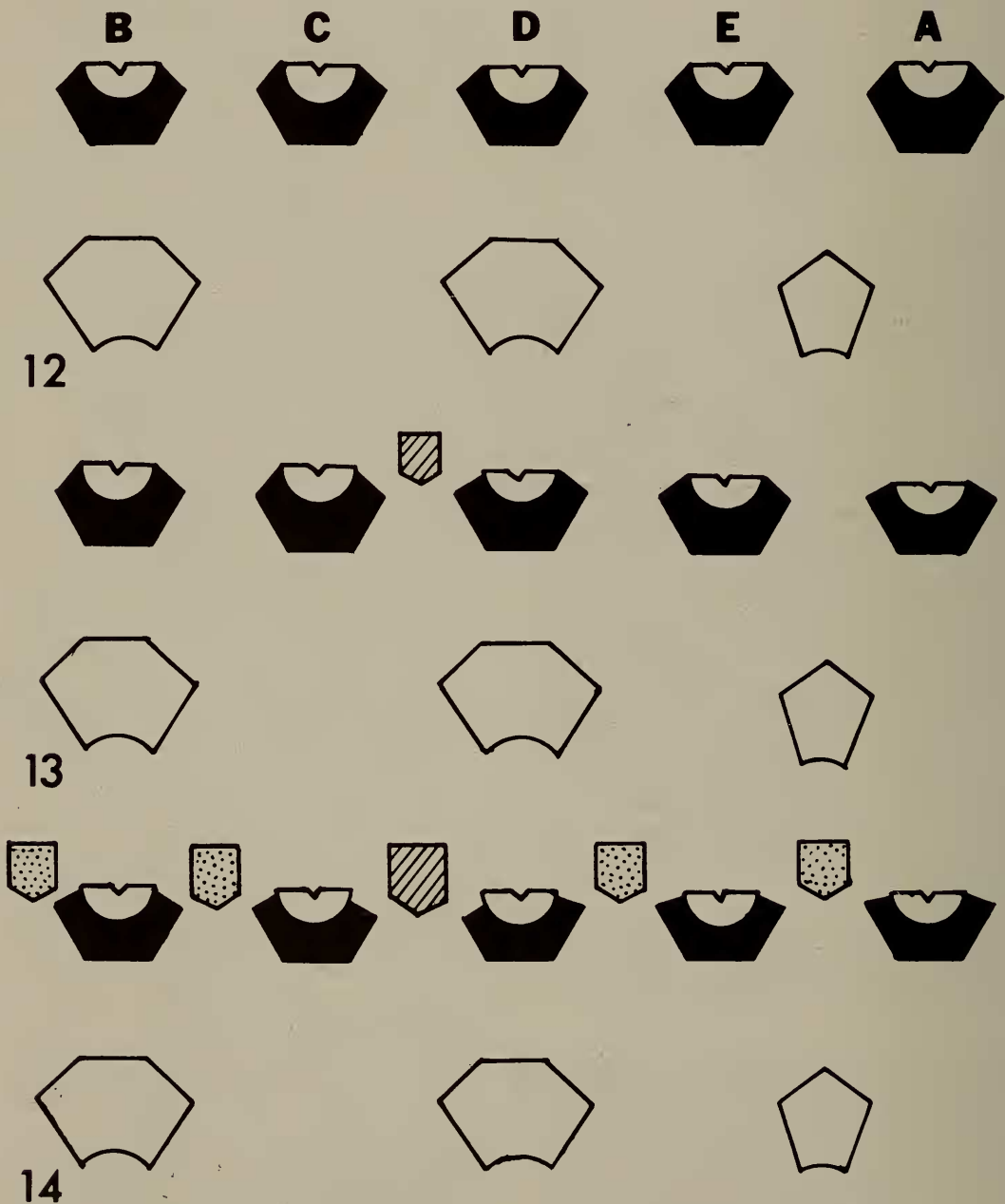
Boucot (1975: 206) interprets the Henryhouse and Waldron brachiopods as quiet water communities. Supporting this assessment are the fine-grained matrix and the abundance of unusually small brachiopod taxa. The suite of genera found in the Waldron sample best fits the *Dicoelosia-Skenidioides* Community of Benthic Assemblage 4 (Boucot, *op. cit.*: fig. 4 and p. 247) and may represent a deeper environment of deposition than does the typical Waldron. All brachiopods recovered are small, *Sphaerirhynchus* is absent and *Atrypa* is rare, while *Dicoelosia*, *Nucleospira*, *Coelospira*, and *Skenidioides* are unusually abundant. *Dalejina*, *Reserella*, *Isorthis*, and *Howellella* are equally represented in both areas. Pelecypods are extremely rare, and few corals are present. Ostracods and bryozoa are most conspicuous in abundance after brachiopods and echinoderms, but sponges are also present. Conodonts are exceedingly rare. Echinoderm genera include common *Stephanocrinus*, *Lecanocrinus pusillus*, "*Deltacrinus*" *stigmatus*, and *Pisocrinus* s. 1. The last has not previously been found in the Waldron; other such genera (besides *Prokopocrinus*) include *Zophocrinus*, an undescribed pygmaecrinid, and *Thalamocrinus*. Many forms common in the typical Waldron are rare or absent here (e.g., *Eucalyptocrinites*, *Macrostylocrinus*, and *Lyriocrinus*) while others which are normally uncommon become relatively abundant (calceocrinids, microcrinoids). Other echinoderms, including *Decaschisma* (Blastoidea) and cyclocystoids, are present in about equal numbers in both.

The Henryhouse *Prokopocrinus*-yield-

ing sample is quite similar. The flexible crinoid *Lecanocrinus* and some inadunates (*Pisocrinus*, *Gissocrinus*) are common, while large camerates are relatively rare. As in the Waldron sample, microcrinoids and calceocrinids are abundant. *Zophocrinus* is among the characteristic genera, while some forms not previously reported from the Henryhouse (undescribed pisocrinid, *Hexacrinites* sp.) are also present. The brachiopod fauna of the Henryhouse

constitutes the only cited example of the *Dicoelosia*—*Orthostrophella* Community (Benthic Assemblage 3) of Boucot (1975: 249) (=Henryhouse Community of Boucot, 1970). Those in our sample show a generic composition and relative abundances much like those in the Waldron sample, from which we have not yet recovered *Orthostrophella*.

The value of the echinoderm taxa as environmental indicators is not well



Figs. 12–14. Plate diagrams showing presumed evolution of the Prokopocrinidae: 12, *Hagnocrinus* (Hirneocrinidae); first interradials (including larger primanal) still notching radials; 13, hypothetical intermediate form with primanal only still in cup; 14, *Prokopocrinus*. Rays lettered according to Carpenter system; basals white, radials black, lateral first interradials stippled; primanal scored obliquely.

established. *Pisocrinus* s.l. occurs in a variety of habitats (Ausich, 1977) but is perhaps most characteristic of moderately deep and quiet water and soft bottoms: Ausich (1977: 684) interprets it as a low-energy rheophile. *Gissocrinus* was found by Lowenstam (1957) to be restricted to less turbulent environments in the northeastern Illinois Silurian. The genus is abundant in the Laurel, the echinoderm-bearing part of which may have been deposited in moderately deep water with relatively weak currents and a slow sedimentation rate (Frest, 1975). It is absent from the Racine reefs but flourishes in the non-reefal Brownsport (Springer, 1926). Certainly its bizarre arm morphology (Springer, 1926: 135–137) is unlikely to be competitive in turbulent environments. Similar conclusions can be drawn from the small inadunates. Breimer and Macurda (1972: 300) suggest that pisocrinids and microcrinoids formed a rheophobic understory in crinoid communities with abundant large rheophiles. Whether these crinoids are termed low-energy rheophiles or rheophobes is primarily semantic; a relatively quiet environment is suggested.

A small sized brachiopod assemblage suggests a soft-bottom, quiet water habitat (Boucot, 1975). Brower (1975) and Watkins and Hurst (1977) interpret Silurian small-sized crinoid assemblages similarly. The latter authors emphasize the soft bottom aspect as the controlling factor (Watkins and Hurst, 1977: 213–216). This is certainly not always the case, as some large camerates like the Silurian-Devonian *Eucalyptocrinites* thrived equally well on soft or hard substrates (Halleck, 1973 and personal observation), while, as acknowledged by Watkins and Hurst (1977: 216), such diverse assemblages as that at Crawfordsville (Lane, 1973) belie the presumed connection between substrate and crinoid size and diversity in the later Paleozoic. Combined with some other factors (mentioned above) the suggestion may have merit.

In the present examples other lines

of evidence can be cited aside from size and substrate. Some of the brachiopods and most echinoderms are disarticulated. No crowns have been recovered and there is little indication that either brachiopods or echinoderms are in life position. This is consistent with a low or moderate rate of sedimentation; transport is here not plausibly a factor of importance. Overall, the evidence suggests a relatively quiet water, soft bottom environment, with sediment accumulation taking place at a moderate depth and at a comparatively slow rate. The similarities between the two faunas (abundant *Pisocrinus*, microcrinoids, and calceocrinids, similar generic composition, with common inadunates and flexibles and scarce camerates; small individuals) may indicate the existence of a discrete assemblage that is a parallel to the brachiopod-based Benthic Assemblage 4 of Boucot; this possibility requires further investigation, however.

Affinities

A crinoid with a plate configuration like that of *Prokopicrinus* could be either an inadunate or camerate. Our choice of the latter, as discussed above, is based in part on the morphology of the basal circlet and even more on the overall resemblance of the genus to some definite camerates (platycrinitaceans, notably the hirneacrinids) and on the reconstruction of phylogenetic trends within the Platycrinitacea. As these have been the subject of 2 recent papers (Brower, 1973; Frest and Strimple, 1977) as well as having been outlined above, the arguments will not be recapitulated here. A tentative phylogeny of the relevant families is presented as Figure 15.

The addition of the Hirneacrinidae and Prokopicrinidae to the picture serves mainly to emphasize the distinctness of the Platycrinitacea from the Patellio-crinacea. The former, including some of the most morphologically specialized (evolutionarily advanced?) camerates, shows a conspicuous tendency toward

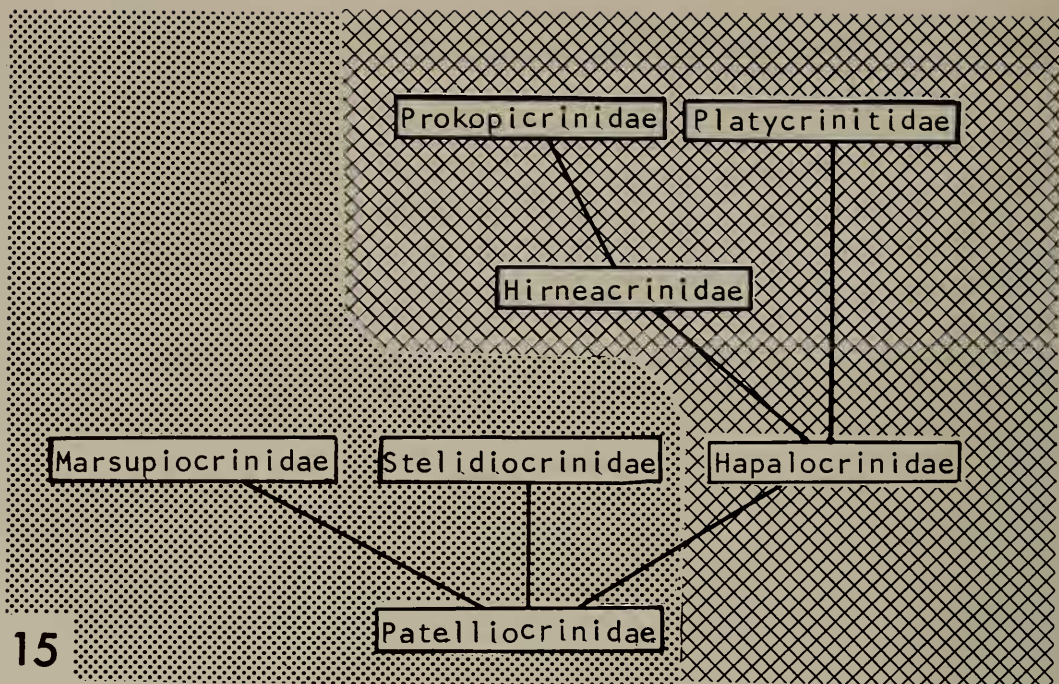


Fig. 15. Possible phylogeny of the patelloiocrinacean and platycrinitacean families. Superfamily Patelloiocrinacea dotted; Platycrinitacea crosshatched.

acquisition of inadunate-like cup [here better termed calyx (Ubaghs, 1978)] features. This divergence from main camerate lines (*i.e.*, crinoids with a many-plated dorsal cup including fixed brachials and numerous plates in inter-radial position) was evidently only partially successful. The early platycrinitacean families (Hapalocrinidae, Hirneocrinidae, and Prokopicrinidae) are, with few exceptions, not particularly diverse or numerous, but the Platycrinitidae are sometimes spectacularly abundant in upper Paleozoic rocks and include many of the last surviving camerates. The superfamily combines the advantages of the inadunate cup (smaller and mechanically more rugged than the typical camerate calyx) with the advanced arm features characteristic of the camerates from their earliest appearance. Once the transition from uniserial or cuneate pinnulate arms to totally biserial was made (in Silurian hapalocrinids) there is little further arm evolution in the superfamily, but the calyx becomes progressively more inadunate-like.

The earliest Patelloiocrinacea (*e.g.*, *Eopatelloiocrinus*) resemble other contemporary camerates, but trends toward

reduction in number of calyx plates and simplification to a patina were initiated very early in the superfamily's history. They are already evident, for example, in the Upper Ordovician *Macrostylocrinus pristinus* (Brower, 1973). Within the Patelloiocrinacea these tendencies are accentuated in the short-lived Marsupioiocrinidae and Stelidiocrinidae; both of these groups, however, retain some fixed IRR and arm brachials, and the marsupioicrinid tegmen is many-plated and without distinguishable orals. Exacerbation of the trend toward expulsion of the IRR led to the development of the Hapalocrinidae, members of which still have one IR series and proximally fixed arms. The hapalocrinid tegmen, while simple in comparison to that of patelloiocrinids, is many-plated and includes both ambulacrals and interambulacrals, as well as distinct orals and the so-called axillary ambulacrals (Breimer, 1962) in some genera. Continued evolution along the same lines resulted in 2 separate lineages. The hirneacrinid lineage, which includes the Prokopicrinidae, rapidly acquired totally free arms and eventually completely eliminated interradianly situated plates

from the calyx. The resultant calyx is fully pentagonally symmetrical and there is no differentiation of the posterior interray. Body volume is reduced, and the tegmen dwindles in size.

In the platycrinid line the tegmen continues to serve a major role. In many Permian and Carboniferous species it is dome-like and rigid, apparently housing part of the body mass as well as the organ systems closely clustered about the mouth. Most platycrinids were robust animals obviously capable of full mucus-net feeding. Some genera and species ultimately considerably simplified the tegmen (*e.g.*, Broadhead & Strimple's [1977] species) but others either retained unchanged or secondarily acquired a hapalocrinid-like tegmen (Breimer, 1962). In contrast to the short-lived specialized Silurian families the Platycrinidae probably represent the main line of evolution in the superfamily and are very likely direct lineal descendants of early Devonian hapalocrinids. Reduction in calyx size, the noted tegmen modifications, and expulsion or elimination of fixed IRR in the Marsupiocrinidae could have produced a form like *Prokopiacrinus*, but no connecting links are known and the hirneocrinid antecedents of the genus can be derived more readily from the Hapalocrinidae. Even fewer steps could produce an identical form from platycrinid predecessors but again no intermediates are presently available: additionally, the oldest undoubted platycrinids are Devonian in age (*Oenochocrinus*). Derivation of the prokopiacrinids from the hirneocrinids would require only continued upward migration of the first IRR, already barely participating in the cup in *Hagnocrinus*. An intermediate step, as yet undiscovered, with only the CD IR (primanal) notching the calyx, is probable (see Figures 12–14).

Similar-appearing forms have been reported among the Inadunata. Some microcrinoids (*e.g.*, *Amphipsalidocrinus*) have comparable plate arrangements, and an *Amphipsalidocrinus*-like form (undescribed) does occur in the Waldron.

However, the microcrinoids, aside from their smaller size, typically have orals that are very prominent and essentially a part of the calyx. Radials are seldom as well developed, many genera are partly or wholly abrachiate, and most have an anal opening in the side of the cup; ontogenies and detailed descriptions of the relevant taxa are in Arendt's (1970) comprehensive monograph. The oldest documented true microcrinoid occurrences are Devonian, but the group is now known to range down into the Ordovician (C. R. C. Paul, personal communication, 1977) and we have Silurian forms from several horizons.

Small Devonian crinoids originally reported as juveniles of the camerate (hapalocrinid) *Cyttarocrinus eriensis* (Hall) by Koenig (1965) have a plate arrangement identical to that of *Prokopiacrinus*. However, the type B (of Ausich, 1977) pisocrinid-like arm facets and fixed orals of these crinoids suggest that they are disparid inadunates related to *Haplocrinites*; this interpretation will be documented in a later paper. These specialized features are not present in the Prokopiacrinidae, thus removing them from consideration as possible antecedents to the Silurian group.

An even more remarkable example of parallel evolution is afforded by the cladid *Elicrinus* (Prokop, 1973) from the Lower Devonian of Bohemia. *Elicrinus* is perfectly pentagonal, has no anal plates, and has a restricted tegmen and prokopiacrinid-like radial arm facets. If the calyx is viewed from above the resemblance to *Prokopiacrinus* is perfect (Prokop, 1973: plate 1, fig. 3). However, *Elicrinus* is dicyclic and cone-shaped (compare figs. 1 and 2); accepting the fundamental nature of the monocyclic-dicyclic "schism" (Warn, 1975) the two cannot be closely related. The problematical nature of any effort to accommodate such superficially simple forms in the present classificatory system is well demonstrated by *Elicrinus*: no evolutionary intermediates are known and the same crinoid could have equally well derived from half a dozen cladid

families. Prokop wisely chose to leave the genus unassigned as to family (1973: 221). Our own procedure here is perhaps rash, but we believe that our case is solid enough to justify more complete treatment than was possible with the dicyclic form.

Yet another possibility is that the known *Prokopicrinus* species are young representatives of an as yet largely undiscovered lineage of true inadunates. Any number of disparid families with documented records extending into the Ordovician or Silurian could have given rise to a prokopicrinid-like form (e.g., the Homocrinidae, Synbathocrinidae, or Ramacrinidae). Again, the problem of missing intermediates prevents resolution of the family's phylogenetic relationships. Whatever the eventual disposition of the group on available evidence, differentiation as a distinct family-level taxon seems inevitable regardless of which alternative progenitor is selected.

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